Ecology, 85(9), 2004, pp. 2616–2629
© 2004 by the Ecological Society of America

COMMUNITY-WIDE IMPACTS OF HERBIVORE-INDUCED PLANT RESPONSES IN MILKWEED (*ASCLEPIAS SYRIACA*)

PETER A. VAN ZANDT[1] AND ANURAG A. AGRAWAL

Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2

Abstract. The effects of early-season herbivory and subsequent induced plant responses have the potential to affect the diversity of herbivorous insect communities. We investigated the seasonal development of the herbivore fauna on common milkweed (*Asclepias syriaca*) to understand the effect of early-season herbivory by different species on insect growth, natural colonization, and community composition. First, we showed that damage by an early-season stem-feeding weevil (*Rhyssomatus lineaticollis*) reduced growth of monarch larvae (*Danaus plexippus*) and leaf beetle larvae (*Labidomera clivicollis*), suggesting that plant quality is reduced by weevil damage. To better understand the potential for initial herbivore damage to affect subsequent colonization by herbivores in the field, we compared undamaged controls to plants experimentally damaged with one of three herbivores: weevils, monarchs, or leaf beetles. We counted seven species of naturally colonizing herbivores on all plants for the next two months to assess colonization, damage, and insect community richness. Our results showed that initial herbivory by different species altered host plant use by herbivores in two years of experiments. Similarly, induced resistance and susceptibility occurred in both years, but due to different initial damaging species on individual plants. Treatment effects also scaled up to alter herbivore community richness. Initial treatments varied in their persistence through the season. For example, in 2001, the influence of initial monarch damage dissipated due to subsequent damage by colonizing herbivores, but the impacts of initial weevil treatment were unaffected. This result suggests that, although induced responses to weevil feeding persisted through the season, monarch herbivory was more likely to affect the herbivore community via a cascade of indirect effects. In 2002, plant and insect responses were more specific, depending on the identity of both initial and colonizing herbivore species. Despite year-to-year variation, considerable consistency in many responses to our treatments indicates that the identity of the initially colonizing herbivore can affect subsequent plant use and community structure. Given the preponderance of influential early-season herbivores, the effects of induced plant responses similar to those presented here may be widespread and may strongly contribute to the structure of phytophagous insect communities.

Key words: Asclepias syriaca; *competition; generalized estimating equations; indirect effects; induced defense; milkweed; plant–insect interactions; Poisson logistic regression; resistance; trait-mediated indirect interactions.*

INTRODUCTION

The composition and structure of herbivorous insect communities can be altered by numerous factors (Karban 1989, Hunter and Price 1992), including bottom-up (Forkner and Hunter 2000, Denno et al. 2002), top-down (Beckerman et al. 1997, Schmitz et al. 2000), and mutualistic (Wimp and Whitham 2001) interactions. Although there has been considerable debate over the relative importance of interspecific competition (Hairston et al. 1960, Lawton and Strong 1981, Karban 1986), such ''lateral'' effects can be a major factor affecting populations and communities of phytophagous insects. For example, a review by Denno et al. (1995) suggested that interspecific competition may not only be more common than previously believed, but may also be a relatively important factor in structuring herbivorous insect communities.

Induced plant responses to herbivory are defined broadly as any modification in the plant following damage, and these include changes in plant quality due to production of toxic or antinutritive compounds, protein or nutritional constituents, leaf toughness, or thorns, spines, or trichomes (Karban and Baldwin 1997). Therefore, induced plant responses provide mechanisms whereby herbivores may compete, either through decreasing the nutritional quality of the plant or by inducing resistance traits (Harrison and Karban 1986, Denno et al. 1995). Induced plant responses may result in competitive interactions more often when the occurrence of two insect species on a host plant are temporally separated (West 1985, Faeth 1986, Karban 1986, Hunter 1987, Denno et al. 1995, 2000, González-

Manuscript received 17 September 2003; revised 27 January 2004; accepted 6 February 2004. Corresponding Editor: R. F. Denno.

[1] Present address: Washington University, Department of Biology, 1 Brookings, Campus Box 1137, St. Louis, Missouri 63130 USA. E-mail: vanzandt@biology2.wustl.edu

Megías and Gómez 2003). Because a large majority of temperate insects exhibit distinct seasonal peaks, with their maximum abundance occurring within a narrow time period (Wolda 1988), there is great potential for early-season herbivores to impact the suitability of host plants for later season species.

The evidence for induced plant responses affecting the preference and performance of subsequent herbivores is accumulating (see previous references, and Haukioja 1980, Karban 1989, Karban and Baldwin 1997, Tscharntke 1999, Denno et al. 2000, Cronin et al. 2001, Wise and Weinberg 2002, Riihimaki et al. 2003). Initial herbivory can affect herbivore communities either through the induction of plant responses (e.g., production of antiherbivore compounds, attraction of natural enemies, or reduction in foliar quality), or through exploitative competition via plant tissue removal (Denno et al. 1995, Hudson and Stiling 1997), and each of these mechanisms may involve several ecological pathways. For example, initial effects may be direct, as with resource exploitation (Hudson and Stiling 1997), or they may be indirect, occurring through interactions with multiple species (Strauss 1991). They may affect the performance (West 1985, Harrison and Karban 1986, Denno et al. 2000), preference (Faeth 1986, Cronin and Abrahamson 2001), or abundance (Hunter 1987, Hudson and Stiling 1997, Thaler et al. 2001) of single or multiple species, and these changes may also translate to alterations in insect community structure such as diversity (Tscharntke 1999, González-Megías and Gómez 2003).

Plant-mediated interactions between herbivorous insects may also be quite specific, with herbivore species causing different responses in host plants and responding to these changes in dissimilar ways (Stout et al. 1998, Agrawal 2000, Agrawal and Karban 2000, Traw and Dawson 2002, Van Zandt and Agrawal 2004). If herbivore-induced plant responses differentially affect subsequently attacking insects on a host plant, then the potential exists for induced responses to affect the resultant herbivore populations and communities (Karban and Baldwin 1997, Underwood and Rausher 2002). While few studies have addressed whether induced plant responses can alter phytophagous insect community structure, to our knowledge none have considered the role of specificity in plant and herbivore responses in affecting phytophagous insect communities.

The main objective of this study was to examine the role of plant responses to different types of early-season herbivory in affecting subsequent herbivore communities. Using a series of field experiments conducted over two years, we tested the hypothesis that early-season herbivory by different herbivores can distinctly affect host plant use by and distribution of individual herbivores, and that these alterations can furthermore alter the community of herbivores on host plants. We test this hypothesis by initially damaging milkweed plants with one of three different herbivores, then following these plants throughout the season. Our goal was to examine whether they differed in the resultant herbivore usage patterns measured as herbivore performance, natural abundance, amount of herbivory, and herbivore species richness per plant.

Methods

Natural history

The common milkweed (*Asclepias syriaca*) is a native weedy perennial that occurs throughout eastern North America in open and disturbed habitats such as roadsides, pastures, and old fields (Uva et al. 1997). Milkweeds possess several putative resistance traits, most notably cardenolides of varying polarity and effectiveness against both specialist and generalist herbivores (Malcolm and Zalucki 1996, Zalucki et al. 2001). Milkweeds received their common name because they exude a sticky, white latex following damage that, in addition to containing high concentrations of cardenolides, serves as a physical barrier to herbivores (Zalucki et al. 2001). Milkweed plants exhibit changes in cardenolide content, latex production, and induced resistance following damage by herbivores, and these responses vary according to the identity of the initial herbivore (Van Zandt and Agrawal 2004; A. A. Agrawal, *unpublished data*).

There are ~12 species of herbivores that consume *A. syriaca* in eastern North America (Seiber et al. 1986, Malcolm et al. 1989), nearly all of which are specialists on *Asclepias* spp. Damage by each of these herbivores is characteristic of the species, due to their different mandibular structures, modes of feeding, and means of circumventing the plant's defensive latex production (Dussourd 1993). In southern Ontario, 10 herbivore species are most commonly observed on milkweed plants (see Plate 1). Of these, monarchs (*Danaus plexippus*), milkweed leaf beetles (*Labidomera clivicollis*), and milkweed tiger moths (*Euchaetias egle*) are folivores. Longhorn milkweed beetles (*Tetraopes tetrophthalmus*) and weevils (*Rhyssomatus lineaticollis*) are folivorous as adults, but larvae feed on rhizomes (Matter 2001) and within the pith of stems (Fordyce and Malcolm 2000), respectively. Milkweed leafminers (*Liriomyza asclepiadis*) feed by consuming tissue between epidermal leaf layers, while small milkweed bugs (*Lygaeus kalmii*) consume developing seeds, and three aphids (*Aphis nerii*, *A. asclepiadis*, and *Myzocallis asclepiadis*) feed on phloem sap. Weevils are active earliest in the season (beginning in May), but they continue to oviposit on plants until July. Monarchs, milkweed beetles, and leaf beetles follow weevils phenologically, and peak in abundance in late July (P. A. Van Zandt and A. A. Agrawal, *personal observations*). The other herbivores are most abundant in the fall.

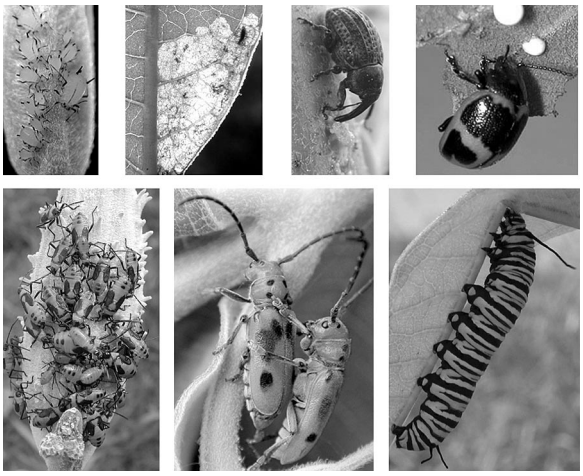

PLATE 1. The milkweed herbivores most commonly encountered in this study included (clockwise, from upper left) aphids (*Aphis nerii*), leafminers (*Liriomyza asclepiadis*), weevils (*Rhyssomatus lineaticollis*), milkweed leaf beetles (*Labidomera clivicollis*), monarchs (*Danaus plexippus*), longhorn milkweed beetles (*Tetraopes tetrophthalmus*), and small milkweed bugs (*Lygeaus kalmii*). Photo credits: A. A. Agrawal and P. A. Van Zandt.

Individual responses: performance of three herbivores on weevil-damaged plants

Because weevils are the earliest herbivores of milkweed at our study location, and because they can have strong impacts on plant survival (Agrawal and Van Zandt 2003), we conducted an experiment to determine if initial damage by weevils substantially reduced the quality of milkweed plants for three species of later season herbivores. This experiment was carried out in three fields: one field of 120 transplanted milkweed plants and two naturally occurring plots of established plants. The planted plot consisted of 4-mo-old plants grown from seed and transplanted to a tilled field, while the other two plots utilized 60 undamaged, naturally growing stems each. All plants were enclosed in spun polyester bags (Rockingham Opportunities Corporation, Reidsville, North Carolina, USA) to impose the weevil damage treatment, exclude naturally colonizing herbivores, and enclose herbivores employed to bioassay plant quality.

To impose the herbivory treatment, we collected adult weevils from field populations and randomly assigned them to half of the plants in each of the three plots. Two adult weevils were introduced to each plant, were allowed to feed and oviposit for four days, and were then removed. It is difficult to determine gender of this species in the field; therefore we added an additional two adults if the original pair had not oviposited after five days. These densities are within the natural range for weevils at this site and season, and this treatment resulted in comparable levels of oviposition scarring to that in nature (see *Results*). Female weevils oviposit within plant stems, and the length of oviposition scars is a reliable predictor of the number of eggs laid per stem ($n = 155$, $r = 0.88$, $P < 0.001$; Agrawal and Van Zandt 2003). Therefore, we measured the length of oviposition scars on weevil-damaged plants as an index of the extent of larval weevil damage. We allowed four weeks for weevil eggs to hatch and for larvae to begin feeding within plant stems, and then assayed equal numbers of plants in all plots with either two leaf beetle larvae, one monarch larva, or two adult aphids (*A. nerii*). For the insect bioassays, we used larvae from maintained colonies, and all bioassays were conducted with neonates that had not fed prior to being placed on experimental plants. For each plant, insects were placed on the undamaged apical leaves and were allowed to move and feed freely on the plant. After four days on treated plants, aphids were enumerated, and beetle and monarch larvae were then removed, dried at 60°C, and weighed to the nearest microgram on a Mettler-Toledo UMT-2 balance (Hightstown, New Jersey, USA). Thus, we had a total of six treatments (damaged or undamaged plants assayed with larval leaf beetles, larval monarchs, or aphids), with $n = 40–42$ per treatment. Herbivores that could not be located were assumed to be dead.

Insect survival and biomass (leaf beetles and monarchs), or population size (aphids) were used as indicators of plant quality. We log-transformed larval mass and aphid number and analyzed them with ANOVA (SAS PROC GLM; SAS 2001) with treatment (weevil damage) as the main effect and plot as a blocking factor. Nonsignificant interactions were excluded from the final model. Separate correlational analyses were conducted to assess the effect of the amount of oviposition damage by weevils on the performance of the three species. Insect survival was analyzed with chi-square tests (SAS PROC FREQ; SAS 2001).

Herbivore population and community responses

To test for the effects of initial herbivory on the development of the subsequent herbivore community, we established experiments in six distinct plots of milkweed plants over two seasons. Treatments on plots were not maintained across years, as aboveground structures die back in the fall. One of the first year's plots (Hill) consisted of 85 plants that had been transplanted from seed, while the other two plots in 2001 (Log and House) and the three studied in 2002 (Rock Ridge, South Road, and Dump) were stems in natural stands of milkweed plants. At each plot we randomly selected ~80 undamaged stems (except for the House plot, which had 60 undamaged stems), then randomly assigned these stems to be controls (no damage) or to receive damage by one of three herbivores: two adult weevils, one monarch larva (third to fifth instar) or four to six leaf beetle larvae. Different numbers of damagers were used per species to approximate the range of natural damage imposed by these insects on field plants. The two folivore treatments, beetles and monarchs, resulted in

large differences in treatment herbivory (number of leaves consumed; 2001, monarchs, 3.45 ± 0.37; leaf beetle, 0.69 ± 0.37; 2002, monarchs, 5.25 ± 0.25; leaf beetle, 1.50 ± 0.25; mean ± 1 SE).

At all plots except Hill, we selected an additional 20 stems that had natural weevil oviposition damage to compare the consequences of our manipulative weevil treatment to the natural pattern in the field. As described previously, we measured the length of oviposition scars. We enclosed all plants except those naturally damaged by weevils in spun polyester bags to contain experimental herbivores and exclude unwanted herbivores. We removed bags and damaging herbivores from each plant as soon as all treatments were imposed. In 2001, plants were sampled every week from 1 August to 12 September, and in 2002 from 10 July to 27 August. This difference between years resulted in a greater number of early-season census periods in 2002, but an equal number of total censuses as the previous year ($n = 7$). Surveys were ended when plants began to senesce and insect populations declined. We utilized a total of 262 stems in 2001 and 309 stems in 2002, partitioned across the five treatments with ~20 replicate stems per treatment per plot per year.

Induced responses in plants can be caused by several factors, including the amount of initial herbivory a plant receives (Agrawal and Karban 2000). To account for differences among treatments in amount of damage imposed, we quantified initial damage and included it as a covariate in all analyses. Initial herbivore damage was scored as the percentage of each leaf that was consumed by an herbivore (visual estimation to the nearest 10%), which was then summed for the whole plant. That is, if there were three leaves damaged 50%, 75%, and 100%, respectively, then that plant would have received an herbivory score of 2.25, meaning that the equivalent of 2.25 leaves had been consumed. This measure is an index of absolute levels of damage, but is highly correlated with percentage herbivory (data from 2002; $n = 1859$, $r = 0.91$, $P < 0.0001$).

We analyzed several variables to characterize population and community responses to initial herbivory. We censused each plant weekly for subsequent herbivory and the presence of naturally colonizing herbivores, beginning one week after we removed the bags. We recorded the presence of all herbivores, constituting seven species, either by visual identification, or by determining the source of new damage to leaves, pods, or stems. Because our measurements of plant usage by herbivores were often based on damage, the population estimates on treatments should be considered relative indices of plant usage, and not estimates of insect population sizes. The three species of aphids were not distinguished, although a majority were *M. asclepiadis*. The amount of herbivory a plant received by colonizing insects and counts of observations of each herbivore species were individually summed across all census periods (not including initial treatment herbivory) for the final analysis, with each plant serving as a replicate and plots as blocks. Because leaf tissue gradually necrotizes near the damaged portion and loses dried latex, which accumulates along the wound, we were able to distinguish new herbivory from prior tissue loss each week. The milkweed tiger moth was observed on only two plants over two years of censusing, and was thus not included in the analyses.

Presence/absence data from our weekly censuses were used to calculate the herbivore species richness for each plant. Average herbivore richness was calculated for each plant as the sum of all weekly herbivore species counts divided by the number of weeks that plant was censused, creating a continuous variable that ranged from 0 to 2.16. We also calculated cumulative herbivore richness as the running total of unique species that utilized each plant. The highest cumulative richness on a stem was seven in 2001, and six in 2002. While cumulative and average richness are positively correlated (2001, $r = 0.82$, $P < 0.0001$; 2002, $r = 0.83$, $P < 0.0001$), they nonetheless represent host plant colonization by herbivores in different ways. A high average richness value could result from two ecological scenarios: either a plant was consistently used by a few species of herbivores or it experienced herbivory by multiple insects at few censuses. Note that because this measure treats all species equally, a plant could have a relatively high average richness if it had the same two species on it every week. Alternatively, cumulative richness represents the number of novel species utilizing each stem. Therefore, while average richness is a general index of plant suitability to one or many herbivores, cumulative richness reflects the usage of that plant by the entire herbivore community.

Repeated plant censusing could potentially result in counting the same insect individuals over successive surveys, thus biasing our estimates of plant use by herbivores. For aphids, this meant that our counts estimated the sizes of aphid populations on plants over time. Leaf miners could be counted accurately without recounting because of their low numbers and persistence on plants. For all other insects except monarchs, there were either too few observations or the feeding individuals were very mobile (e.g., *Tetraopes* adults), and therefore repeated counting of individuals was unlikely. To estimate the magnitude of repeated counting for monarch larvae, we reviewed data from the plot most used by monarchs. We totaled all of the observations of monarch eggs or larvae, only including observations of individuals (i.e., not including presence due to herbivory alone). The total number of cases where the same monarch individual could have been counted over successive weeks was 33/134 surveys (24.6%). Because this is a very conservative estimate of repeated counting (i.e., it assumes that *all* cases where individual monarchs are seen over two census periods are the same individual, which is unlikely), the impact of true recounting was much lower. While this

level of recounting could lead to a slight bias in the estimation of plant colonization by monarchs, it does not affect estimates of herbivory or average or cumulative richness.

Population and community responses: statistical methods

Continuous responses that could be normalized (plant damage, average herbivore richness) were log-transformed (after adding one to each value) to improve homoscedasticity, and were analyzed with ANOVA (SAS PROC GLM; SAS 2001). Back-transformed values are presented in the text and figures where noted, and therefore represent geometric mean values. Tukey adjusted post hoc contrasts were performed between all levels of initial herbivore treatment.

Dichotomous and count variables (cumulative richness and presence/absence of herbivore species) were analyzed with Poisson logistic regression using generalized estimating equations (GEE–PROC GENMOD; Allison 1999, Stokes et al. 2000, SAS 2001). We analyzed presence/absence data of colonizing herbivore species in two ways. In the first analysis, we summed observations across all census periods for each plant, creating an aggregate count of plant use by different species. For example, if monarchs were found on a plant at three censuses and *Tetraopes* for two censuses, that plant would have a value of three for monarchs and two for *Tetraopes*. We then used logistic regression on the counts of each responding species to determine which species were more abundant on plants following initial treatment. For the second analysis, we retained the raw structure of the presence/absence data and analyzed weekly observations with repeated-measures logistic regression (PROC GENMOD). Results were very similar to the previous analysis, so except where noted, only those results from the aggregate data are presented. For all analyses, we included interactions between plot and treatment in initial models, but removed these terms when interaction P values were >0.1. There were never enough data for repeated-measures analyses to include interactions between time and any main effects. We also used initial herbivore treatment damage and plant height as covariates to account for differences in amount of herbivory caused by different treatments and effects of differential attractiveness of different sized plants, but only included these effects when they were significant at $P < 0.1$.

While herbivore treatments could differ in their effects on subsequent herbivores, we were also interested in determining whether this was due to lasting effects of the initial treatment per se, or because of damage subsequent to, but affected by the initial treatment (i.e., a cascade of indirect effects set off by initial damage). We used repeated-measures logistic regression, both with and without the previous week's herbivory due to colonizing herbivores as a covariate, to determine if subsequent herbivory affected the strength of the initial treatment over the rest of the season. Analyses where the effects of initial herbivore treatment were no longer significant after the inclusion of subsequent herbivory were interpreted as evidence for indirect effects following the initial treatment causing the observed response. In contrast, analyses where treatment effects remained significant despite the inclusion of subsequent herbivory as a covariate indicated a lasting effect of initial herbivory per se.

In our Poisson logistic regression analyses of presence/absence, cumulative richness, and count data, results indicate the relative number of species or individuals on a plant due to plot and treatment (initial herbivore species) effects. Logistic regression produces an odds ratio for each level of every factor adjusted for other terms in the model, which indicates the odds (or likelihood) of the response occurring. Odds ratios are statistically compared to one (equal likelihood of the event occurring in each case); therefore, values less than one indicate decreased odds and values greater than one indicate increased odds relative to a reference level.

We compared the census data over the two years statistically for abundance of different herbivores, average and cumulative richness, and herbivory by colonizing insects. Herbivore abundance and cumulative richness were analyzed with logistic regression, while average richness and herbivory were compared with ANOVA. Due to strong differences among years in these responses, and because of differences in the timing of experiments and in the populations of plants studied, we conducted all analyses separately for each year.

RESULTS

Induced responses at the individual level: performance of three herbivores

Monarch larval mass was 22% lower on weevil damaged plants compared to undamaged plants ($F_{1,34} = 4.72$, $P = 0.038$), but leaf beetle larval mass ($F_{1,23} = 0.69$, $P = 0.41$) was not affected by weevil treatment (df differed for each assay insect due to varying levels of survival/recovery). Neither monarch nor leaf beetle survival was affected by initial weevil damage (monarchs, $\chi^2 = 1.3$, $P = 0.25$; leaf beetle, $\chi^2 = 0.3$, $P = 0.87$). Similarly, aphid numbers on weevil-treated plants did not differ from controls (weevil treatment, 8.56 ± 1.62 individuals; controls, 7.11 ± 1.61 individuals; $F_{1,71} = 0.45$, $P = 0.51$; mean $\pm$ 1 SE). Among plants damaged by weevils, the amount of oviposition scarring (an index of the number of feeding larvae) showed negative trends with insect performance for leaf beetles ($r = -0.018$, $P = 0.003$), but not for monarch mass ($r = -0.002$, $P = 0.58$) or aphid numbers ($r = -0.046$, $P = 0.26$).

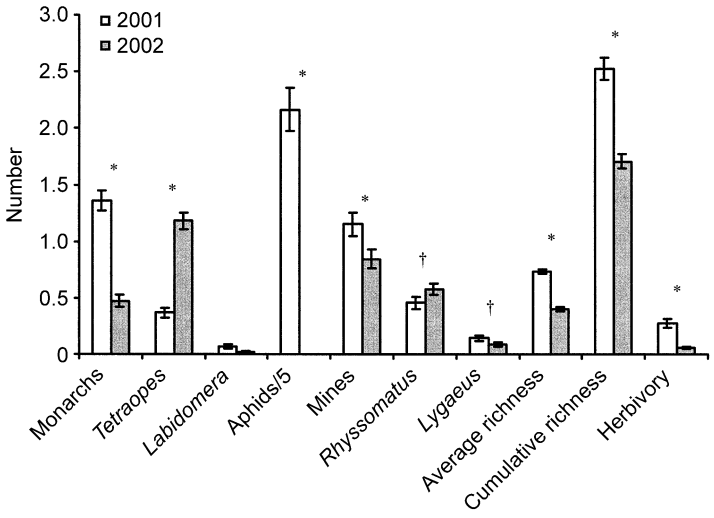

FIG. 1. Herbivore abundance/responses across years for all treatments combined. Data for each colonizing herbivore species or for herbivory are means of summed values for each plant over the entire season, with differences represented by a dagger (†) for $P < 0.1$, and by an asterisk (*) for $P < 0.05$. Average richness and subsequent herbivory were compared across years with ANOVA, and herbivore species abundances were analyzed with Poisson logistic regression. Herbivory was measured as the proportion of each leaf that was damaged and therefore represents the number of leaf equivalents that were consumed by herbivores (e.g., one leaf consumed received a value of 1). Herbivore richness as represented here was calculated as the average number of herbivore species occurring on a plant over all census periods. Aphid numbers are represented as one-fifth of the total abundance to fit them on the same *y*-axis. Error bars are ±1 SE.

Induced responses at the population level: colonization of plants by herbivores

There was considerable variation among years in the abundance of the seven herbivore species, most notably for monarchs, *Tetraopes*, and aphids (Fig. 1). In both years, herbivores were generally more often found on taller plants (Table 1). In 2001, monarchs avoided weevil-damaged plants, but colonized monarch-damaged plants over twice as often as controls (Table 1). Similarly, *Tetraopes* were over three times more abundant on monarch-damaged plants than controls. *Tetraopes* also avoided plants experimentally damaged by weevils compared to monarch-treated plants, and did not distinguish between plants naturally and experimentally damaged by weevils. In addition, plants experimentally damaged by weevils had approximately 66% fewer monarchs and aphids, but nearly 90% more weevils than controls in 2001. While plants naturally damaged by weevils were never different from controls in terms of herbivore colonization, they also did not differ significantly from plants experimentally treated with weevils.

In 2002, the trends for overall abundance (Fig. 1) and plant use by herbivores (Table 1) were reversed from the previous year. The most abundant herbivores in 2001 (aphids and monarchs) declined by 99% and

TABLE 1. Odds ratios representing the relative numbers of colonizing herbivores based on the influence of initial treatment (plants damaged by natural weevil colonists, or experimentally added [''Expt.''] weevils, monarchs, or leaf beetles), relative to control (initially undamaged) plants in 2001 and 2002.

Responding species	Initial treatment				Height		Overall treatment effect	
	Monarch	Leaf beetle	Natural weevil	Expt. Weevil	χ^2	P	χ^2	P
2001 community								
Monarchs	2.37* a	1.75 a	0.74 b	0.32* b	4.01	0.045	34.92	<0.0001
Aphids	0.70 ab	1.37 a	0.64 ab	0.37* b	0.88	0.35	14.07	0.0071
Leaf miners	1.34 a	1.19 a	0.34 b	0.71 ab	0.57	0.45	13.73	0.0082
Lygaeus	0.63	0.55	1.38	0.50	4.22	0.04	2.35	0.67
Weevil	1.49	1.40	2.48	1.88*	0.55	0.46	5.28	0.26
Tetraopes	3.31* a	1.55 ab	1.34 ab	0.55 b	0.01	0.91	16.66	0.0022
2002 community								
Monarchs	0.41	0.61	0.64	0.68	19.07	<0.0001	4.32	0.36
Leaf miners	0.48† a	0.43 a	1.83 b	0.51 a	8.48	0.004	15.38	0.004
Lygaeus	0.72	1.76	4.10	2.12	3.03	0.08	7.40	0.12
Weevil	1.52 a	0.91 b	3.15* a	2.73* a	1.76	0.18	18.75	0.0009
Tetraopes	0.45	0.59	1.02	0.54	12.87	0.0003	8.90	0.06

Notes: Models included plant height as a covariate where its effect was significant at $P < 0.1$. Analysis was conducted with Poisson logistic regression on counts of total numbers of insects occurring on plants throughout the season. Odds ratios <1 indicate fewer herbivores, while values >1 indicate increased numbers of herbivores compared to control plants. Significant values are indicated as follows: † $P < 0.1$; * $P < 0.05$. Unique letters beside table entries indicate significant differences among initial treatments in all pairwise comparisons. Post hoc comparisons were only made where the overall treatment effect was <0.05. Alpha levels for the comparison of all responses were adjusted using a sequential Bonferroni correction for multiple unplanned comparisons. Chi-square values and the corresponding *P* values are also reported for the main overall effect of treatment. There were too few observations of aphids in 2002 for analysis.

65%, respectively. While monarchs were generally less abundant on all treated plants relative to controls in 2002, they were 66% less abundant on monarch-treated plants compared to controls, and were marginally less frequent on plants naturally damaged by weevils compared to controls (Table 1). Leaf miners were also less than half as common on monarch- or leaf beetle-damaged plants as on controls, and marginally less abundant than on plants naturally damaged by weevils. Furthermore, weevils were roughly three times more common on both naturally and experimentally weevil-damaged plants than on controls or plants treated with leaf beetles. *Tetraopes* were marginally less likely to be found on monarch-treated plants as controls, again in contrast with the previous season; however, they did not distinguish among other treatments in post hoc comparisons (Table 1). Aphids were not sufficiently abundant in 2002 to be analyzed.

We used repeated-measures logistic regression to determine if damage by colonizing herbivores altered the strength of the initial treatment over the rest of the season. Results from this analysis in both years were consistent with the results of the previous analysis. The one exception was for aphids in 2001, where the repeated-measures analysis indicated, that in addition to being negatively impacted by plants experimentally damaged by weevils, aphids were also less abundant on plants initially damaged by monarchs and naturally weevil-damaged plants (whole model with herbivory as a covariate $\chi^2 = 20.69$, $P = 0.0004$). In 2001, the inclusion of herbivory by colonizing insects diminished the effect of initial monarch treatment for both monarch and *Tetraopes* presence (effect on monarchs without herbivory covariate, $P = 0.0265$, and with herbivory covariate, $P = 0.30$; effect on *Tetraopes* without herbivory covariate, $P = 0.079$, and with herbivory covariate, $P = 0.58$), indicating that subsequent herbivory attenuated initial treatment effects. In contrast, the initial influence of weevils on the abundance of monarchs, aphids, and leaf miners was only slightly augmented with the inclusion of subsequent herbivory, and the effects of weevils on these colonizers remained significant ($P < 0.05$ for monarchs, aphids, and weevils).

In 2002, the inclusion of subsequent herbivory caused changes in the initial treatment effects that varied according to the identity of the responding species. For plants treated with monarchs, subsequent herbivory by colonizing insects diminished initial treatment effects on *Tetraopes* (without herbivory covariate, $P = 0.056$ and with herbivory covariate, $P = 0.23$), but did not affect monarch colonizers ($P = 0.075$, both with and without subsequent herbivory covariate). On plants naturally damaged by weevils, subsequent herbivory clarified the effect of initial treatment on monarchs (without herbivory covariate, $P = 0.084$ and with herbivory covariate, $P = 0.034$), but diminished treatment effects on weevils (without herbivory covariate, $P = 0.005$ and with herbivory covariate, $P = 0.20$). On plants experimentally damaged by weevils, subsequent herbivory also reduced the effects of treatment on weevil abundance (without herbivory covariate, $P = 0.034$ and with herbivory covariate, $P = 0.42$). Leaf miners could not be analyzed with repeated measures in either year, so the effects of subsequent herbivory could not be examined. Plot and time effects were frequently significant, indicating that herbivore presence varied through the season and in different habitats ($P < 0.05$ in most analyses; results not shown). However, the interaction between treatment and plot was never significant ($P > 0.2$).

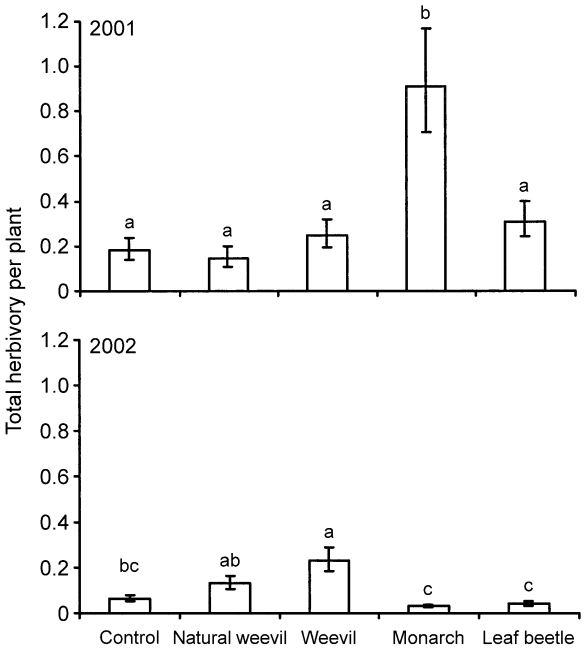

FIG. 2. Herbivory following treatment for undamaged plants (control), plants damaged by natural weevil colonists, or by experimentally added weevils, monarchs, or leaf beetles. Data are back-transformed least-square means from analysis with plot and treatment as main effects. Herbivory was estimated as in Fig. 1. Bars with different letters are different in Tukey adjusted post hoc comparisons. Error bars are ±1 SE.

Induced responses at the community level: herbivore damage

The amount of herbivory on plants was roughly three times greater in 2001 than in 2002 (Fig. 1). In 2001, subsequent herbivory by naturally colonizing insects differed among treatments (Fig. 2; $F_{4, 254} = 7.24$; $P < 0.0001$) and plots ($F_{2, 254} = 41.55$; $P < 0.0001$). Neither the plot × treatment interaction nor the extent of initial herbivory were significant in 2001 ($P > 0.5$ for both), so they were not included in the final model. Monarch-treated plants received nearly five times more herbivory than control plants, but all other treatments received similar amounts of herbivory as controls. Leaf beetle-

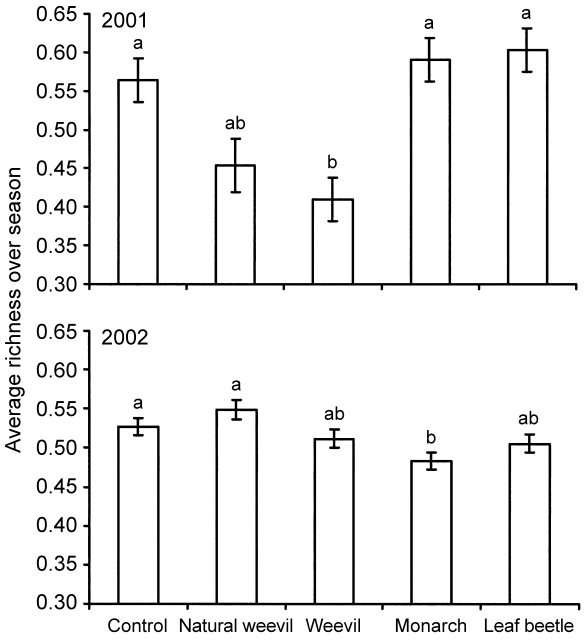

FIG. 3. Effect of treatments on average insect richness measured as the average across all weeks for the total number of insects that used each host plant throughout two seasons on undamaged plants (control), plants damaged by natural weevil colonists, or by experimentally added weevils, monarchs, or leaf beetles. Data are least-square means from analysis with plot and treatment as main effects. Bars with different letters are different in Tukey adjusted post hoc comparisons. Error bars are ±1 SE.

treated plants received 1.7 times more herbivory than did controls (Fig. 2), but this difference was not significant.

In 2002, herbivory by colonizing insects again differed among initial treatments (Fig. 2; $F_{4, 294} = 13.23$, $P < 0.0001$) and plots ($F_{2, 294} = 6.86$, $P = 0.0012$). The plot × treatment interaction was significant in 2002 ($F_{8, 294} = 2.03$, $P = 0.042$), so it was included in the final model. The amount of initial herbivory was not a significant covariate ($P > 0.2$). Plants experimentally treated with weevils had over three times greater herbivory than control plants in 2002 and over seven times more damage than monarch-treated plants, but did not differ from plants naturally damaged by weevils.

Induced responses at the community level: herbivore richness

Both average species richness and cumulative richness per plant differed substantially between years, with 2001 having 2.75 times greater cumulative richness than 2002 (Fig. 1). Within each season, plants treated with damage by different initial herbivores had different numbers of species subsequently colonize compared to controls, as measured by both average (Fig. 3; 2001, $F_{4, 254} = 8.91$, $P < 0.0001$; 2002, $F_{4, 283} = 4.22$, $P = 0.0025$), and cumulative (Fig. 4; 2001, $\chi^2 = 26.47$, $P < 0.0001$; 2002, $\chi^2 = 24.15$, $P < 0.0001$) richness. Plots also differed strongly in average (2001, $F_{2, 254} = 47.72$, $P < 0.0001$; 2002, $F_{2, 283} = 14.67$, $P < 0.0001$) and cumulative (2001, $\chi^2 = 7.61$, $P = 0.022$; 2002, $\chi^2 = 47.56$, $P < 0.0001$) species richness, but the plot × treatment interaction was not significant in either year for either response ($P > 0.10$ for both responses and years). Initial treatment herbivory was not a significant covariate for either cumulative or average richness in either year ($P > 0.2$); however, plant height covaried positively with average ($F_{1, 285} = 22.55$, $P < 0.0001$) and cumulative ($\chi^2 = 18.17$, $P < 0.0001$) richness in 2002.

Similar to the results for average species richness, plants that received the most subsequent damage in general also had the highest cumulative herbivore richness, while those treatments with the least damage had the lowest cumulative herbivore richness. In 2001, plants initially damaged by weevils had ~16% lower average herbivore richness throughout the season than did plants initially damaged by monarchs or leaf beetles, and 14% lower than undamaged controls (Fig. 3). Monarch- and leaf beetle-treated plants also had the greatest number of colonizing herbivore species in 2001, measured as cumulative richness, accumulating

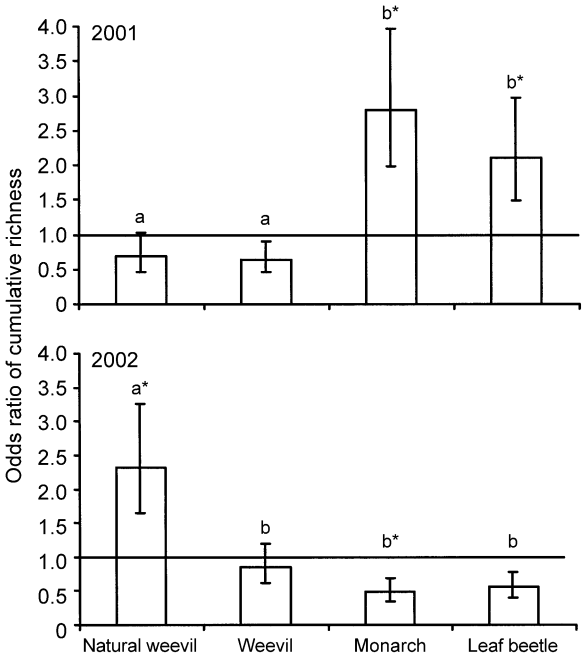

FIG. 4. Effect of treatments on cumulative herbivore richness measured as the running total of insects that used each host plant throughout the season on plants damaged by natural weevil colonists, or by experimentally added weevils, monarchs, or leaf beetles. Data are odds ratios from logistic regression analysis with plot and treatment as main effects. Odds ratios <1 indicate fewer herbivores, while values >1 indicate increased numbers of herbivores compared to control plants (line = 1). Bars with unique letters differ in planned comparisons, and asterisks (*) after letters indicate differences from controls ($P < 0.05$). Error bars are ±1 SE.

over twice as many herbivore species as the other three treatments (Fig. 4). Leaf beetle-treated plants received approximately the same average number of species throughout the season as did control or monarch-damaged plants (Fig. 3), and accumulated the same number of novel herbivore species as monarch-treated plants (Fig. 4).

While plants in 2002 treated with different initial herbivores also differed in average species richness, the patterns were reversed from 2001 (Fig. 3). Monarch-treated plants were the only group to differ from undamaged controls for average herbivore richness, with 9% fewer species than controls, and >12% fewer herbivore species than plants naturally damaged by weevils. The differences are more striking for cumulative richness, where monarch- and leaf-beetle treated plants accumulated only 44% and 60%, respectively, the number of herbivore species as controls (Fig. 4). In contrast to both of these results and those in 2001, plants naturally damaged by weevils had over twice the cumulative species richness as any other treatment (Fig. 4), and monarch-treated plants accumulated only ~40% as many herbivore species as controls.

With the exception of cumulative richness in 2002, plants naturally damaged by weevils did not differ from experimentally treated plants in either average damage or richness for both years (Figs. 2 and 3), suggesting that differences in host choice by weevils or in experimental manipulations were unimportant for these responses. Similarities in responses between plants naturally colonized and experimentally damaged by weevils could also be due to similar levels of oviposition damage (least squared mean ± SE; naturally damaged, 71.4 ± 5.01 cm; experimentally damaged, 84.3 ± 6.14 cm; $F_{1, 170} = 2.67$, $P = 0.10$).

Discussion

Although induced plant responses are apparently ubiquitous and have strong consequences for plant fitness (Agrawal 1998), their roles in affecting insect populations and communities are still unknown (Karban and Baldwin 1997, Underwood and Rausher 2002). Whether they involve changes in resistance traits such as secondary chemicals (e.g., Agrawal and Kurashige 2003), or alterations in plant nutrition (e.g., Denno et al. 2000), induced plant responses provide mechanisms whereby herbivores may compete (Harrison and Karban 1986, Denno et al. 1995), and are therefore a type of trait-mediated indirect interaction (Werner and Peacor 2003). Furthermore, these competitive effects may be apparent later in the season (reviewed in Denno et al. 1995), or over subsequent seasons (reviewed in Karban and Baldwin 1997) or plant generations (Agrawal 2001). Many induced responses exhibit considerable specificity, with herbivores causing different host plant reactions, and responding uniquely to these responses (Stout et al. 1998, Agrawal 2000, Agrawal and Karban 2000, Traw and Dawson 2002, Van Zandt and Agrawal 2004). Given that plant responses differentially affect insect herbivore species, the potential exists for induced responses to affect the resultant herbivore populations and communities (Tscharntke 1999, González-Megías and Gómez 2003).

When we compared the performance of three herbivore species on undamaged plants and plants experimentally damaged with weevils, we found that monarchs grew ~22% slower on weevil-damaged plants than on controls. In addition, the performance of all three herbivores tended to decline with increasing weevil oviposition. However, not all of the insects responded similarly, thus demonstrating specificity of herbivore response to the initial damage. These findings, together with previous results showing that monarch larval growth is decreased by ~20% when feeding on plants previously damaged by monarchs or leaf beetles (Van Zandt and Agrawal 2004), demonstrate that initial herbivory affects individual herbivore performance on milkweed plants, but that the responses vary with responding species. From these results, we predicted that if herbivores avoid plants that they perform poorly on, then they should be less abundant on weevil-treated plants.

Effects of induced plant responses on natural abundances and community parameters

Plants initially treated with different herbivores differed from control plants in the numbers of herbivore colonists that utilized them (Table 1), indicating that initial herbivory can alter host plant usage; however, population responses were not all in the same direction for each herbivore. In general, monarchs and most other herbivores avoided plants damaged by weevils, consistent with induced resistance demonstrated in the individual level experiment. In contrast, weevils were attracted to plants initially damaged by weevils, suggesting induced susceptibility. Increased densities of weevils are not likely due to aggregation pheromones present in other weevil species (Rochat et al. 1991), as movement in *R. lineaticollis* is not related to weevil density, either among or within patches (St Pierre and Hendrix 2003). The apparently idiosyncratic responses demonstrate additional specificity in plant and insect responses to damage in this system (Van Zandt and Agrawal 2004), and further illustrate that weevils can be one of the most influential herbivores in this plant–herbivore association (Agrawal and Van Zandt 2003).

Our finding of monarchs heavily utilizing monarch and leaf beetle damaged plants in 2001 is unexpected, given previous results (Van Zandt and Agrawal 2004). Foraging and oviposition preferences do not always agree with larval performance on host plants (Cronin and Abrahamson 2001), and monarchs apparently also fail to accurately oviposit on less resistant hosts. For example, monarchs do not discriminate between oviposition on the high cardenolide *A. curassavica* and the low cardenolide *A. incarnata* (Zalucki et al. 1990).

However, Zalucki et al. (1990) observed that females preferred plants with intermediate (200–400 μg/0.1 g dry mass) cardenolide levels. It is therefore possible that since monarchs sequester cardenolides most efficiently in this range (Malcolm 1995), they may be trading off larval performance on higher cardenolide plants in favor of protection from predation (Zalucki et al. 2001).

Plants initially treated with different herbivores also showed considerable variation in the amount of herbivory they received (Fig. 2). In the first year of the study, monarch-treated plants showed induced susceptibility toward subsequent herbivores. A post hoc inspection of the data (not shown) along with results from Table 1 indicated that much of this herbivory was by monarch larvae. In the second year, herbivory overall, as well as on monarch-treated plants was considerably lower (Figs. 1 and 2). This is likely an indication of the low population sizes that year, due to a catastrophic die-off of monarchs in early 2002 at their overwintering grounds in Mexico (Brower et al. 2004). The large impact of monarch damage in 2001 on subsequent herbivory and richness demonstrates the wide-ranging effects of monarch population fluctuations, as well as the sensitivity insect communities can exhibit to environmental disturbances across the continent.

Data for both years also supported the hypothesis that initial herbivory could alter herbivore community richness. We characterized herbivore communities using both average and cumulative richness, and both measures were affected by initial treatment. Average richness is an index of average plant use, but it does not differentiate between observations of individuals of one species and members of different species. In contrast, cumulative richness emphasizes members of different species, but ignores much of the dynamics of herbivore usage of plants over the season. An examination of these two measures together yields a clearer picture. In 2001, control plants had high average richness but low cumulative richness, indicating that most of the herbivory on control plants was due to consistent usage by a few species. Monarch- and leaf beetle-treated plants had both high average and cumulative richness, indicating a consistent usage by many species. The similar results for beetle and monarch treatments were despite large differences in initial (treatment) herbivory, suggesting that folivores may affect plants differently than do pith feeding weevils. Furthermore, the similarity in responses suggests that specificity in the latex response of plants to herbivory by these two species (Van Zandt and Agrawal 2004) does not translate into differences in field colonization. Natural and experimentally weevil-treated plants had both low average and cumulative richness; therefore both individuals and species avoided them. In 2002, control, experimental weevil, and leaf beetle plants had high average richness, but low cumulative richness, indicating that the same species utilized these plants through the season. High cumulative and average richness on plants naturally damaged by weevils suggests that these plants were attractive to multiple species while low richness values for monarch-damaged plants indicate that they were avoided by multiple species. Induction treatments caused changes in the cumulative species richness of colonizing herbivores by one or two species; while this effect appears small, this comprises a majority of the relatively small and specialized herbivore community. Although up to 12 species are potential herbivores of milkweed in northeastern North America, the realized number of species in these communities was much lower: seven species in 2001 and six species in 2002.

The resultant herbivore community on each of these treatments could also have been a function of altered visitation of plants by all insects or due to one species being uniquely deterred or attracted to a treated plant. The population responses of each of the herbivores (Table 1) suggest that increases in cumulative richness on monarch- and leaf beetle-treated plants in 2001 were largely due to attraction of monarch, leaf miner, weevil, and *Tetraopes* herbivory, indicating that no single herbivore species caused the observed increases in cumulative richness. Similarly, the low average richness on experimental weevil-treated plants in 2001 and monarch-treated plants in 2002 was because all herbivores except weevils were deterred from visiting these plants. Finally, the high cumulative richness on plants naturally damaged by weevils in 2002 was also due to increased attraction of multiple herbivores. Therefore, changes in richness were due to wholesale responses by most of the herbivore community, but the direction of the responses was driven by the identity of the initial herbivore.

One other factor that may be important in determining plant use by herbivores is indirect defenses via natural enemies (Dicke 1999). Our experiments were not conducted to ascertain the effects of indirect defenses, and natural enemies could have been differentially attracted by our initial treatments. However, with the exception of monarch larvae, we observed very few instances of natural enemy attack. An analysis of monarch egg abundance agrees qualitatively with the results of larval monarch abundance (not shown). Even if indirect defenses are altered by initial damage in this system, the conclusions that initial herbivory affects resultant herbivore communities and that the identity of the initial herbivore is important are not changed.

Few studies have experimentally examined the influence of initial herbivory on the response of the entire herbivorous community. Marquis and colleagues (Wold and Marquis 1997, Lill and Marquis 2003) conducted experiments on early-season white oak (*Quercus alba*) herbivory, and found that early-season leaf tying by *Pseudotelphusa* sp. strongly influenced community composition on trees (Lill and Marquis 2003), while general herbivory and hole punching did not (Wold and

Marquis 1997). González-Megías and Gómez (2003) removed all adults of the monophagous beetle, *Timarcha lugens*, from its host plant and observed a subsequent increase in arthropod richness for two of three years. From these results, along with those of the present study, it is clear that initial herbivory can substantially affect subsequent host plant use by herbivores. However, the challenge for understanding the role of plant mediated competition in phytophagous insect communities lies in identifying the complexity that arises due to herbivore specificity, as well as uncovering general patterns among different early-season herbivores. In this study, we did not monitor putative resistance traits; therefore we cannot determine why initial damage by some species resulted in different levels of plant usage by the resultant community. However, other studies have demonstrated that cardenolide and nitrogen concentrations, latex production, and stem thickness can each influence herbivore performance and colonization of these milkweeds (Malcolm 1995, Zalucki et al. 2001, Agrawal and Van Zandt 2003, Agrawal 2004, Van Zandt and Agrawal 2004; Lavoie and Oberhauser, *in press*). Moreover, these traits not only vary genetically, but also show specificity of response following damage by different species (Van Zandt and Agrawal 2004; A. A. Agrawal, *unpublished data*). Therefore, specific changes in any of these plastic traits could be responsible for observed differences among species treatments.

Variation between years

One potential reason that results of this study differed between the two years lies in the differences in the abundance of some herbivores, most notably aphids and monarchs (Fig. 1). In other studies, variation in the relative strength of competitive effects or host plant use have been found to be due to changes in other biotic or abiotic factors (Karban 1989, Cronin et al. 2001). Insect populations are inherently variable, and this variation may be caused by several factors (Gaston and McArdle 1994). In our study, these may include factors such as a local buildup (in 2002) of an exotic lady beetle population introduced to control aphids in the surrounding agricultural areas. On a continental scale, monarchs experienced low population sizes, likely due to a catastrophic die-off in their overwintering grounds in Mexico (Brower et al. 2004). Both aphids and monarchs were common on plants in 2001 and declined sharply in 2002. Because this study site is at the northern limits of the monarch's distribution and these sites are recolonized every year from long-distance migrants, substantial year-to-year fluctuations in monarch abundance are common (Urquhart 1987). In turn, the deficiency of these species likely reduced the cascade of indirect effects demonstrated in this study and may have been responsible for the lower species richness measurements in 2002. Methodologically, the major differences between years were that different patches of plants were used in 2002, and the season began and ended earlier in that year. However, neither of these was likely to lead to the variation in responses, as responses were consistent among sites and censusing was ceased early in 2002 because plants had begun to senesce.

What then do the results from this study say regarding the importance of induced responses in affecting herbivorous insect communities? First, several consistent patterns are still evident from our results. With the exception of cumulative richness in 2002, naturally and experimentally weevil damaged plants are always similar in responses. Weevils were more abundant on weevil-treated plants than controls in both years, and monarchs always avoided weevil-treated plants relative to controls (Table 1). These results suggest that weevils were not merely selecting host plants of a particular quality, but that weevil adult and larval feeding altered host plant traits to make them less attractive to monarchs and more attractive to weevils. Furthermore, the two most abundant folivores, *Tetraopes* and monarchs, differed from controls in the same way across years, suggesting the potential for generalizing herbivore responses to early-season herbivory. Also, monarchs and aphids were less common on weevil-damaged plants, which is consistent with their performance in the first experiment. Therefore, initial herbivory can be a consistent influence on subsequent herbivores despite substantial yearly variation in herbivore abundance.

More generally, because initial herbivore treatments affected species' use of host plants, plant damage, and insect community richness in both years, we can conclude that induced plant responses can have important impacts on members of the herbivore community in natural field settings. However, the variation in the magnitude and direction of species responses suggests that the effects of initial herbivory on insect communities are sensitive to other interacting factors and that their outcomes are therefore not predictable at our current level of understanding. Given the considerable variation in responses for such a small herbivore community, it is possible that consistent results will only be observable in communities with fewer interactions. Future work on this question should attempt to identify what other factors are important in determining host plant usage and herbivore community structure.

Ecological pathways for community effects of induced plant responses

Our initial treatments could affect colonization by herbivores in two different ways: either directly by altering plant suitability for all subsequent herbivores, or indirectly by initiating cascades of interactions among colonists. Indirect interactions could occur by a chain of responses that followed initial treatment, similar to the successional processes of facilitation, tolerance, or inhibition (Connell and Slatyer 1977). Indirect effects, where interactions between two species

are altered by the presence of others, are common in community ecology (Strauss 1991). To separate these two alternatives, we partitioned out significant treatment effects into the initial treatment per se and indirect effects following the initial treatment by including subsequent herbivory as a covariate in our repeated-measures analysis. In 2001, all initial effects of monarchs dissipated due to subsequent herbivory, while the impact of weevil damage persisted. Initial damage by natural weevils and monarchs reduced monarch colonization in 2002, and these effects were evident throughout the season. However, the effects of both natural weevil and monarch treatments (in addition to those of the experimental weevil treatment) dissipated in their impacts on colonizing weevils and *Tetraopes* with subsequent herbivory. While some treatments acted through either direct or indirect means depending on year (monarch effects on monarch colonists, and weevil effects on weevil colonists), others were consistently direct (weevil effects on monarch colonists) or indirect (monarch effects on *Tetraopes* colonists). The variation in these results suggests that other variables likely determine whether the initial treatment acts directly or indirectly on herbivore community succession, but that both pathways may be influential.

Competition between herbivores

In the past 20 years, interspecific competition has been rediscovered as an important factor for phytophagous insects (West 1985, Faeth 1986, Karban 1986, Hunter 1987, Denno et al. 1995, González-Megías and Gómez 2003), and our results suggest that it can also affect herbivore community structure through host plant modification by initial herbivory. We have demonstrated that initial herbivory can influence subsequent herbivore performance, host plant use, and community richness; however we did not observe consistent patterns over seasons or among groups of herbivores. Further effort will be required to determine generalities in insect–insect interactions mediated through host plants. Identifying herbivores that alter communities via plant mediated competition may face the same difficulties as determining keystone species a priori (Power et al. 1996), but likely candidates include early-season species and those that substantially alter plant architecture or quality (e.g., Denno et al. 2000, Lill and Marquis 2003).

Because monarchs, weevils, and to a lesser extent, leaf beetles, impact subsequent herbivores, plant traits that alter attractiveness to initial herbivory may be important factors in setting up the initial cascade of insect responses. For example, stem thickness (Agrawal and Van Zandt 2003) and cardenolide concentration (Malcolm and Brower 1986) are important oviposition cues for weevils and monarchs, respectively. In other studies, we have found genetic variation among full-sibling families of milkweed for trichome density, leaf toughness, nitrogen content, latex production, and other traits which may influence herbivory (A. A. Agrawal, *unpublished data*). Thus, variation in a variety of genetically and environmentally influenced traits may translate into variation in herbivore community structure and plant use via effects on early-season herbivory.

Acknowledgments

We thank G. Cox, J. Dodgson, K. Edwards, N. Griffiths, N. Kurashige, C. Griffin, L. Plane, K. Rotem, D. Viswanathan, and J. Jensen for help with the experiments. J. Chase, J. Kneitel, M. Gibbons, J. Thaler, D. Viswanathan, K. Smith, R. Denno, and two anonymous reviewers provided helpful comments on the manuscript. This research was supported by NSERC of Canada, the Canadian Foundation for Innovation, and a Premier's Research Excellence Award from the government of Ontario.

Literature Cited

Agrawal, A. A. 1998. Induced responses to herbivory and increased plant performance. Science **279**:1201–1202.

Agrawal, A. A. 2000. Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. Oikos **89**:493–500.

Agrawal, A. A. 2001. Transgenerational consequences of plant responses to herbivory: an adaptive maternal effect? American Naturalist **157**:555–569.

Agrawal, A. A. 2004. Resistance and susceptibility of milkweed to herbivore attack: consequences of competition, root herbivory, and plant genetic variation. Ecology **85**: 2118–2133.

Agrawal, A. A., and R. Karban. 2000. Specificity of constitutive and induced resistance: pigment glands influence mites and caterpillars on cotton plants. Entomologia Experimentalis et Applicata **96**:39–49.

Agrawal, A. A., and N. S. Kurashige. 2003. A role for isothiocyanates in plant resistance against the specialist herbivore *Pieris rapae*. Journal of Chemical Ecology **29**:1403–1415.

Agrawal, A. A., and P. A. Van Zandt. 2003. Ecological play in the coevolutionary theatre: genetic and environmental determinants of attack by a specialist weevil on milkweed. Journal of Ecology **91**:1049–1059.

Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Sciences (USA) **94**:10735–10738.

Brower, L. P., D. R. Kust, E. Rendon-Salinas, E. G. Serrano, K. R. Kust, J. Miller, C. F. d. Rey, and K. Pape. 2004. Catastrophic winter storm mortality of monarch butterflies in Mexico in January 2002. *In* K. M. Oberhauser and M. Solensky, editors. The monarch butterfly: biology and conservation. Cornell University Press, Ithaca, New York, USA, *in press*.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119–1144.

Cronin, J. T., and W. G. Abrahamson. 2001. Goldenrod stem galler preference and performance: effects of multiple herbivores and plant genotypes. Oecologia **127**:87–96.

Cronin, J. T., W. G. Abrahamson, and T. P. Craig. 2001. Temporal variation in herbivore host-plant preference and performance: constraints on host-plant adaptation. Oikos **93**: 312–320.

Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces

mediate natural-enemy impact in a phytophagous insect community. Ecology **83**:1443–1458.
Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects—competition reexamined and resurrected. Annual Review of Entomology **40**: 297–331.
Denno, R. F., M. A. Peterson, C. Gratton, J. A. Cheng, G. A. Langellotto, A. F. Huberty, and D. L. Finke. 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. Ecology **81**: 1814–1827.
Dicke, M. 1999. Evolution of induced indirect defense of plants. Pages 62–88 *in* R. Tollrian and C. D. Harvell, editors. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.
Dussourd, D. E. 1993. Foraging with finesse: caterpillar adaptations for circumventing plant defenses. Pages 92–131 *in* N. E. Stamp and T. M. Casey, editors. Caterpillars: ecological and evolutionary constraints on foraging. Chapman and Hall, New York, New York, USA.
Faeth, S. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. Ecology **67**: 479–494.
Fordyce, J. A., and S. B. Malcolm. 2000. Specialist weevil, *Rhyssomatus lineaticollis*, does not spatially avoid cardenolide defenses of common milkweed by ovipositing into pith tissue. Journal of Chemical Ecology **26**:2857–2874.
Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology **81**:1588–1600.
Gaston, K. J., and B. H. McArdle. 1994. The temporal variability of animal abundances: measures, methods and patterns. Philosophical Transactions of the Royal Society of London, Series B **345**:335–358.
González-Megías, A., and J. M. Gómez. 2003. Consequences of removing a keystone herbivore for the abundance and diversity of arthropods associated with a cruciferous shrub. Ecological Entomology **28**:299–308.
Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.
Harrison, S., and R. Karban. 1986. Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. Oecologia **69**:354–359.
Haukioja, E. 1980. On the role of plant defences in the fluctuation of herbivore populations. Oikos **35**:202–213.
Hudson, E. E., and P. Stiling. 1997. Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia*. Oikos **79**:521–528.
Hunter, M. D. 1987. Opposing effects of spring defoliation on late season oak caterpillars. Ecological Entomology **12**: 373–382.
Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders—heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**: 724–732.
Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. Ecology **67**:1063–1072.
Karban, R. 1989. Community organization of *Erigeron glaucus* folivores: effects of competition, predation, and host plant. Ecology **70**:1028–1039.
Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.
Lavoie, B., and K. M. Oberhauser. *In press*. Varying nitrogen content of *Asclepias syriaca* (Gentiales: Asclepiadaceae) and its effect on *Danaus plexippus* (Lepidoptera: Nymphalidae) consumption rates and performance. Environmental Entomology.
Lawton, J. H., and D. R. Strong. 1981. Community patterns and competition in folivorous insects. American Naturalist **118**:317–338.
Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology **84**:682–690.
Malcolm, S. B. 1995. Milkweeds, monarch butterflies, and the ecological significance of cardenolides. Chemoecology **5–6**:101–117.
Malcolm, S. B., and L. P. Brower. 1986. Selective oviposition by monarch butterflies (*Danaus plexippus* L.) in a mixed stand of *Asclepias curassavica* L. and *Asclepias incarnata* L. in south Florida (USA). Journal of the Lepidopterists' Society **40**:255–263.
Malcolm, S. B., B. J. Cockrell, and L. P. Brower. 1989. Cardenolide fingerprint of monarch butterflies reared on common milkweed, *Asclepias syriaca* L. Journal of Chemical Ecology **15**:819–853.
Malcolm, S. B., and M. P. Zalucki. 1996. Milkweed latex and cardenolide induction may resolve the lethal plant defence paradox. Entomologia Experimentalis et Applicata **80**:193–196.
Matter, S. F. 2001. Effects of above and below ground herbivory by *Tetraopes tetraophthalmus* (Coleoptera: Cerambycidae) on the growth and reproduction of *Asclepias syriaca* (Asclepidacae). Environmental Entomology **30**: 333–338.
Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience **46**:609–620.
Riihimaki, J., P. Kaitaniemi, and K. Ruohomaki. 2003. Spatial responses of two herbivore groups to a geometrid larva on mountain birch. Oecologia **134**:203–209.
Rochat, D., C. Malosse, M. Lettere, P. H. Ducrot, P. Zagatti, M. Renou, and C. Descoins. 1991. Male-produced aggregation pheromone of the American palm weevil, *Rhynchophorus palmarum* (L) (Coleoptera, Curculionidae): collection, identification, electrophysiological activity, and laboratory bioassay. Journal of Chemical Ecology **17**:2127–2141.
SAS. 2001. SAS/STAT software; version 8.2. SAS Institute, Cary, North Carolina, USA.
Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist **155**:141–153.
Seiber, J. N., L. P. Brower, S. M. Lee, M. M. McChesney, H. T. A. Cheung, C. J. Nelson, and T. R. Watson. 1986. Cardenolide connection between overwintering monarch butterflies from Mexico and their larval food plant, *Asclepias syriaca*. Journal of Chemical Ecology **12**:1157–1170.
Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. Categorical data analysis using the SAS system. SAS Institute, Cary, North Carolina, USA.
Stout, M. J., K. V. Workman, R. M. Bostock, and S. S. Duffey. 1998. Specificity of induced resistance in the tomato, *Lycopersicon esculentum*. Oecologia **113**:74–81.
St Pierre, M. J., and S. D. Hendrix. 2003. Movement patterns of *Rhyssomatus lineaticollis* Say (Coleoptera: Curculionidae) within and among *Asclepias syriaca* (Asclepiadaceae) patches in a fragmented landscape. Ecological Entomology **28**:579–586.
Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. Trends in Ecology and Evolution **6**:206–210.
Thaler, J. S., M. J. Stout, R. Karban, and S. S. Duffey. 2001. Jasmonate-mediated induced plant resistance affects a community of herbivores. Ecological Entomology **26**:312–324.

Traw, M. B., and T. E. Dawson. 2002. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants. Environmental Entomology **31**:714–722.

Tscharntke, T. 1999. Insects on common reed (*Phragmites australis*): community structure and the impact of herbivory on shoot growth. Aquatic Botany **64**:399–410.

Underwood, N., and M. Rausher. 2002. Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. American Naturalist **160**: 20–30.

Urquhart, F. A. 1987. The monarch butterfly: international traveler. Wm Caxton, Ellison Bay, Wisconsin, USA.

Uva, R. H., J. C. Neal, and J. M. DiTomaso. 1997. Weeds of the Northeast. Comstock Publishing Associates, Ithaca, New York, USA.

Van Zandt, P. A., and A. A. Agrawal. 2004. Specificity of induced plant responses to specialist herbivores of the common milkweed, *Asclepias syriaca*. Oikos **104**:401–409.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083–1100.

West, C. 1985. Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. Ecological Entomology **10**:111–120.

Wimp, G. M., and T. G. Whitham. 2001. Biodiversity consequences of predation and host plant hybridization on an aphid–ant mutualism. Ecology **82**:440–452.

Wise, M. J., and A. M. Weinberg. 2002. Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. Ecological Entomology **27**:115–122.

Wold, E. N., and R. J. Marquis. 1997. Induced defense in white oak: effects on herbivores and consequences for the plant. Ecology **78**:1356–1369.

Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics **19**:1–18.

Zalucki, M. P., L. P. Brower, and S. B. Malcolm. 1990. Oviposition by *Danaus plexippus* in relation to cardenolide content of 3 *Asclepias* species in the southeastern USA. Ecological Entomology **15**:231–240.

Zalucki, M. P., S. B. Malcolm, T. D. Paine, C. C. Hanlon, L. P. Brower, and A. R. Clarke. 2001. It's the first bites that count: survival of first-instar monarchs on milkweeds. Austral Ecology **26**:547–555.